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From the hereditary standpoint, color and size characters in either plants or animals are not equally well understood. In general, the inheritance of color, technically known as a qualitative character, has been rather satisfactorily determined. On the modern chromosome theory of heredity, the genetic factors responsible for the development of colors appear to be located on the various chromosomes of the species and apparently follow a regular, stable and predictable mode of inheritance from generation to generation. Environmental agencies play a relatively minor part in modifying such characters. It is for this reason, perhaps, that their inheritance has been so thoroly investigated.

However, with respect to size characters, technically known as quantitative characters, the exact mode of inheritance is still somewhat uncertain. Presumably this is due to the complexity of these characters and to their marked susceptibility to environmental influence. The multple-factor hypothesis, which is the most reasonable explanation of quantitative inheritance at the present time, is still in need of verification. Also the manner in which genetic factors for size react in the development of such quantitative characters needs explanation.

Perhaps one of the most direct means of actually testing whether quantitative inheritance depends upon the same hereditary mechanism as does qualitative inheritance is by determining the presence or absence of genetic linkages between these two sorts of characters. If they are dependent on the same mechanism of heredity, cases should be found in which size and color are genetically associated with each other because their factors are carried on the same chromosome. It seems reasonable to suppose that in the evolution of varieties of plants or breeds of animals, certain major factors for size may have become very closely associated on the chromosomes with certain color factors, in which case appropriate hybridization experiments should bring out this correlation.

[1]Paper No. 8 from the Department of Genetics, Iowa State College, Ames, Iowa.

It was thought that the tomato (*Lycopersicum esculentum* Mill.), because of its natural method of close self-pollination and its commercial development into many varieties, with a good assortment of sizes of fruits and colors, would offer a splendid chance to test such a situation. Accordingly, numerous pure varieties of tomatoes with different colors and sizes of fruit were crossed in various combinations. The general plan was to make sets of varietal crosses in the following manner:

1. *Large red* x *small yellow.*
2. *Small red x large yellow.*

In these crosses large size is in one case contributed by a red variety, while in the other by the yellow parental variety. It is in this manner only that color and size associations, if found, can be differentiated as to their cause, since any correlation discovered may be either *physiological* or *genetical,* broadly speaking. For example, if it were found that red color and large size were always correlated in tomatoes, the cause might be conceived as the physiological one of the red color itself being in some way more conducive to greater size of fruit. However, if it could be shown that red color is correlated with greater size only because it happened that the red parental variety carried the larger size, then obviously the cause would seem to be a genetical one. Actually to prove the existence of such a genetic association of color and size, it would be necessary to show that greater size could be associated with *yellow* color whenever yellow color and large size were contributed by the same parental variety. Accordingly, it is essential that such combinations of crosses as are listed in the illustration be investigated.

There are relatively few published records of genetic correlations or linkages between qualitative and quantitative characters in plants or animals. Hoshino (2) reported a possible case in peas wherein there seemed to be an association between flower color and time of flowering. To the wrtier's knowledge the cause of this correlation has never been determined. Halsted (1) in a cross of two varieties of tomatoes gave some F_2 data in which there was a slight association of flesh color and size of fruit. At that time no logical interpretation of this situation was made and the correlation was reported only in one direction. Warren (9) in an analysis of egg-size inheritance in *Drosophila melanogaster,* found that certain factors controlling egg size were linked with qualitative factors located on all of the chromosomes in this species of insect.

In the garden bean (*Phaseolus vulgaris*) both Sax (5) and Sirks (7) have demonstrated that a correlation between size and color exists, wherein weight of beans is apparently correlated

with color in the seed coat. Appropriate crosses were not made to differentiate this correlation on a physiological or genetical basis, however. A preliminary report, Lindstrom (3), on work with the tomato pointed clearly to a correlation between size of fruit and skin color. This situation has now been enlarged and the earlier results verified. In addition, the relation between size factors and flesh color of the fruit has been investigated and critical data are now available.

MATERIAL AND METHODS

Using commercial varieties of tomatoes that had been under experimental control for one generation before the cross-pollinations were effected, the following nine crosses involving different colors and sizes of fruit were successfully made reciprocally, and hybrid generations from them studied:

1. *Red Cherry* (*small*) x *Golden Beauty* (*large*)
2. *Bonny Best* (*large*) x *Yellow Peach* (*medium*)
3. *New Globe* (*large*) x *Yellow Cherry* (*small*)
4. *John Baer* (*large*) x *Yellow Peach* (*medium*)
5. *Red Cherry* (*small*) x *Yellow Peach* (*medium*)
6. *Dwarf Giant* (*large*) x *Yellow Peach* (*medium*)
7. *John Baer* (*large*) x *Golden Beauty* (*large, but smaller than John Baer*)
8. *Dwarf Giant* (*large*) x *Yellow Cherry* (*small*)
9. *Bonny Best* (*large*) x *Yellow Cherry* (*small*)

Most of the original crosses were made in the field and were properly bagged after emasculation and pollination. Some of the backcrosses were made in the greenhouse and in this case the flowers were not bagged. The individual plants under these circumstances were kept separately in various corners of the greenhouse and it is believed that contamination could not have occurred. Because of the large number of characters that differentiated the parental varieties, it may be stated that any effects of contamination would soon have become noticeable.

Plantings were made both in the greenhouse and in the field. Greenhouse plants were eventually potted in eight inch pots, using uniformly mixed soil. In all cases the potting was done the same day. Care was taken to provide as nearly equal conditions of light and temperature as was possible, by dint of frequent shiftings to different parts of the bench. The plants were staked and trained to a single stem. The growing tip was pruned after three to five clusters of fruits had set. Despite these precautions, it is felt that environmental conditions in the

greenhouse, where two or three hundred plants are being grown at one time, are exceedingly difficult to equalize.

Field plants were started in the greenhouse and, on being transplanted, were carefully regulated as to spacing, replication and treatment. All transplanting from greenhouse to field was done the same day. Rows were three and a half feet apart and plants in the rows three feet apart. About the middle of August (after five or more clusters had set fruit) the plants were severely pruned so that individual notes could be taken with greater certainty. No other pruning or training was resorted to in the field.

Color notes were checked by the writer and by an assistant independently. The blooming date was determined daily by noting the opening of the first flower in the first cluster. Fruits were measured (polar and equatorial diameters) with a caliper, and readings taken to the nearest millimeter. Weights of individual fruits were taken to the nearest gram. Ordinarily from three to five representative fruits were chosen from a single plant for measurements and weights. More fruits were used in cases of obvious irregularity in fruiting. The assistants were carefully instructed to choose average fruits. Specific gravity of the fruit was determined in some instances. After all the notes were taken, an observational check on fruit size and color was made on the remaining fruits so as to catch any very evident misjudgment*.

COLOR INHERITANCE

Prior to any discussion of the relation between color factors and quantitative characters it is essential that a brief summary statement be made as to the heredity of color in the tomato. A full report of the genetics of fruit color in this species has appeared in a recent paper (Lindstrom, 1925). Subsequent to this work, additional data have accumulated that will be included herein.

Fruit color of tomatoes depends primarily on two pairs of hereditary factors, *Rr* and *Yy*. Dominant *R* is responsible for red flesh color, whereas the recessive *r* factor, when homozygous, produces the yellow flesh color, due presumably to the absence of the reddish, needle-shaped pigment crystals present in the red fleshed varieties. Dominant *Y* controls the formation of a distinct yellow pigment residing in the epidermal cell walls, while

*At one time or another during the progress of these experiments the following graduate students in genetics have assisted: Mr. K. M. Liu, Mr. C. S. McClesky, Mr. M. R. Irwin, and Mr. G. H. Rieman. Dr. W. A. Carver also helped with the earlier cross-pollination work and measurements.

Table I SUMMARY OF COLOR INHERITANCE IN THE TOMATO
-F_2 generations of varietal crosses

Crosses	RY Orange-red	Ry Pink	rY Dark yellow	ry Pale yellow	Difference 10:6 basis
Type -F_2 (RY x ry)					
From table II (Lindstrom 1925)*	294	90	75	26	
Red Cherry x Yellow Peach	122	49	43	12	
John Baer x Golden Beauty	26	13	11	2	
John Baer x Yellow Peach	85	23	31	6	
Total observed	527	175	160	46	5.5 ± 9.8
Total expected	511	170	170	57	
Type -F_2 (Ry x rY)					
From table II (Lindstrom 1925)*	84	25	20	8	
Red Peach x Golden Fig	36	9	12	3	
Total observed	120	34	32	11	-7.9 ± 4.6
Total expected	111	37	37	12	

gene *y* produces a colorless or transparent condition of the cell walls of the fruit skin or epidermis. For all practical purposes, both *R* and *Y* exhibit complete dominance.

Such a situation provides for four basic color combinations characteristic of all tomato fruits, as follows:

RY—orange-red (red flesh showing thru yellow skin)

Ry—light red, pink or "purple" (red flesh unobscured by any skin color)

rY—dark yellow (yellow both in flesh and skin)

ry—pale yellow (yellow flesh showing thru a colorless epidermis)

Genes *R* and *Y* appear to be inherited independently of each other, that is, they are borne on different chromosomes. Data to support this statement are to be found in tables I and II. In table I there are F_2 data arising both from the crosses *RR YY* x *rr yy*, and *RR yy* x *rr YY*.

Apparently there is no evidence of linked inheritance here since a 9:3:3:1 phenotypic, F_2 ratio of the four fruit color combinations is very closely approximated. With a total of 1105 F_2 plants the deviations from expectancy on the basis of independent inheritance were comparatively insignificant. The same conclusion may be more readily drawn from the series of backcrosses shown in table II, where 1 : 1 : 1 : 1 ratio of the four color types is so closely approached among a total of 920 plants.

There is accordingly ample justification for believing that genes *Rr* and *Yy* are carried on different pairs of chromosomes

*Summary from a previous publication.

Table II. SUMMARY OF COLOR INHERITANCE IN THE TOMATO
Data from backcrosses of various dihybrid F_1 plants on the double recessive types.

Crosses	RY Orange-red	Ry Pink	rY Dark yellow	ry Pale yellow	Difference 1:1 basis
Type F_1 (RY x ry) x ry					
From table III (Lindstrom 1925)*	112	93	93	94	
(Bonney Best x Yellow Peach) x Golden Beauty	15	18	12	16	
(Dwarf Giant x Yellow Peach) x Yellow Peach	30	29	28	33	
(Dwarf Giant x Yellow Peach) x Golden Beauty	40	42	32	31	
Total observed	197	182	165	174	
Total expected	179.5	179.5	179.5	179.5	12 ± 9.0
Tpye F_1 (Ry x rY) x ry					
From table III (Lindstrom 1925)*	35	38	30	26	
(New Globe x Yellow Cherry) x Golden Beauty	18	18	17	20	
Total observed	53	56	47	46	
Total expected	50.5	50.5	50.5	50.5	-2 ± 4.8

in the tomato. As far as is known, there are no other qualitative genes on these chromosomes at the present time since it has been established, Lindstrom (4), that the dwarf (d) and "peach" (p) factors are independently inherited of both of the color factors. These two genes have been found to be linked, and data taken on some of the crosses reported herein have shown only three non-parental or cross-over types in a total of 119 plants. This gives a crossover percentage of 2.5, indicating that the *d* and *p* factors are not completely linked as was found to be true in the carlier report.

RELATION OF COLOR AND SIZE FACTORS

Experiments involving the color factor pairs *Rr* and *Yy*, and various sizes of tomato fruits were planned so as to test any relation existing between these two sorts of characters. Size of fruit of a plant was determined by weight, number of seed locules, and polar and equatorial diameters. Because of the high correlation existing between weight of fruit and the other physical characters, the following discussions will center on fruit weight primarily, altho data for the other characters are also presented.

Three of the most important crosses will be discussed individually, the others being grouped into a miscellaneous class.

*Summary from a previous publication.

RED CHERRY X GOLDEN BEAUTY CROSS

The varietal cross Red Cherry x Golden Beauty gave the most striking data on the problem. In this case the cross was made reciprocally between these commercial varieties, and the parental, F_1, F_2 and backcross generations grown in the field during the same season (1923). Red Cherry (*RR YY*) is a very small, early type, extremely uniform in fruit size. Under the field conditions of this experiment its average fruit weight was 7.3 ± 0.3 grams. The Golden Beauty (*rr yy*) parent was somewhat later and more variable and had a mean fruit weight of 166.5 ± 6.4 grams. The first hybrid generation (F_1) of this cross and its reciprocal, carrying the color genes *Rr Yy*, averaged 23.9 ± 0.4 grams in weight. This indicates an appreciable dominance of the smaller fruit type. This F_1 generation was backcrossed to the medium-sized Yellow Peach variety (*rr yy*, average weight 51.0 grams) and also to the parental Golden Beauty variety. Data from these two backcross generations and the F_2 generation are arranged in table III in such a manner as to show the average weight of fruit for each of the two pairs of color factors in these hybrid generations.

Were there no relation between color and size, the F_2 and backcross generation fruits of any color type should exhibit approximately the same average weight. Apparently there is no great difference in the average weight of fruits with red flesh (*R*) as compared with those of the yellow flesh (*r*) color. It is true that in all three hybrid generations in table III, the yellow-fleshed fruits (r) are slightly heavier. The differences, however, are in no case statistically significant. Nevertheless, the mere fact that in all three hybrid generations the yellow fruits are consistently heavier would seem to indicate that the *r* color factor, contributed by the larger Golden Beauty parent (*rr yy*), was associated with the larger fruit weight, if only to a slight extent. It is not desired to stress this linkage or correlation, if

Table III. HYBRID GENERATIONS OF THE RED CHERRY (SMALL) x GOLDEN BEAUTY (LARGE) CROSS SHOWING AVERAGE WEIGHT (GRAMS) OF FRUITS IN RELATION TO FLESH AND SKIN COLOR

Generation	Flesh color			Skin color		
	R	r	Difference	Y	y	Difference
F_2 generation RR YY x rr yy	26.0±0.7	32.6±2.9	6.6±3.0	23.6±0.6	38.3±2.1	14.7±2.2
No. of plants	81	18		75	24	
F_1 x Yellow Peach	36.1±1.1	36.6±1.2	0.5±1.6	29.4±0.7	44.0±1.2	14.6±1.4
No. of plants	78	46		66	58	
F_1 x Golden Beauty	63.0±3.2	64.7±2.4	1.7±4.0	51.2±2.0	79.2±2.8	28.0±3.4
No. of plants	32	28		33	27	

existent, because the other color factors, *Y* and *y*, exhibit such a very significant relationship with weight and serve to emphasize the point at hand.

Considering now the relation between skin color (controlled by genes *Y* and *y*) and weight, it is obvious that in all three hybrid generations the fruits with the colorless or transparent skin type are consistently heavier. The difference in average fruit weight of the *Y* and *y* color classes are so marked and so consistent that mere inspection of the data is sufficient to pronounce them significant. In all three progenies, the colorless-skinned fruits are approximately 50 percent larger than the yellow-skinned fruits. When the probable errors of these differences are considered, all three show that they could not reasonably be attributed to chance.

Thus it is evident that the recessive, colorless-skin factor *y* is closely associated with a greater weight of fruit in this cross. As the data now stand, it would be possible for physiological relation to exist between these two characters so that colorless skin itself might be directly responsible for increased fruit weight. From the data given under the Bonny Best x Yellow Peach cross, however, it will be shown that the colorless-skinned fruits in that cross are *smaller* than those with the yellow skin, thus demonstrating that the casual relation is not essentially physiological, but is genetical. In other words, the recessive *y*-type fruits of the Red Cherry x Golden Beauty cross are larger presumably because the Golden Beauty parent contributed both the *y* color factor and certain hereditary factors for larger size. On the chromosome theory of heredity, the same chromosome that bears *y* carries a linked factor (or factors) for greater size, whereas the color allelomorph *Y* is on an homologous chromosome also bearing one or more factors for smaller fruit.

The relations between the *Yy* color genes and size are somewhat more easily visualized when they are plotted as frequency curves as has been done in fig 1 for the three hybrid generations.

It is interesting to observe that in all three cases there are definite indications of segregation for size differences. This is especially true in the backcross generations, where several distinct modes appear, indicating perhaps the existence of major genotypes for size of fruit. These are somewhat obscured in the F_2 generation by the skewness of the curve occasioned no doubt by the partial dominance of small size, and yet it may clearly be seen that the great majority of the smaller fruited plants are those with the dominant *Y*-type of skin. These evidences of size segregation are being studied in detail, but it is not the object of the present report to analyze the inheritance of size as such.

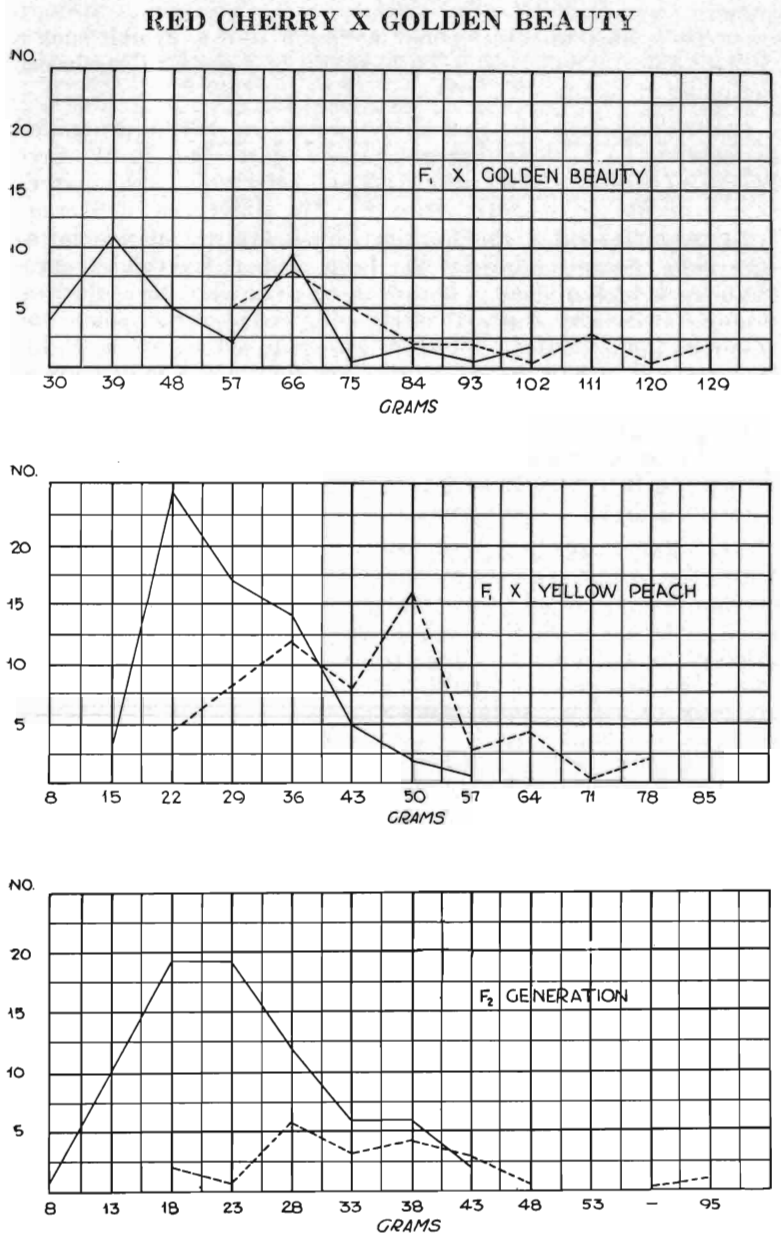

Fig. 1. Frequency curves of tomato weights in grams classed according to skin color types. Solid line represents dominant Y (yellow) skin and dotted line, recessive y (transparent) skin.

Table IV. RELATION OF SKIN COLOR FACTORS TO OTHER CHARACTERS IN THE RED CHERRY x GOLDEN BEAUTY CROSS

Generations	Days to flowering		Number locules		Polar diameter mm.		Equatorial diameter mm.	
	Y	y	Y	y	Y	y	Y	y
F_2 generation	78.4	80.5	2.9	3.3	30.4	35.4	34.8	41.2
F_1 x Yellow Peach	78.5	80.7	3.0	3.0	32.7	36.9	37.8	43.6
F_1 x Golden Beauty	77.7	80.0	3.8	4.1	37.7	43.7	46.8	55.1

In order to confirm the findings with weight in relation to the skin color factors, table IV has been prepared in which other characters, such as days to flowering (time of opening of the first flower in the first cluster), number of seed locules, polar and equatorial diameters of the fruits are arranged according to the skin color classes in the same three hybrid generations discussed in the preceding paragraphs. In this table, there is the same consistent difference with respect to the color factors, namely that the colorless-skinned fruits (y) have the largest measurements. This perhaps is to be expected since number of locules, polar and equatorial diameters are correlated with fruit weight.

The physiologist on seeing that the y-type of fruits flowered later than the Y-type might deduce that therein lay the causal agency that produces larger fruits with the colorless skin, since lateness is very often associated with relatively larger size in plants. In order to show that there is no inherent influence of time of flowering on weight of fruit, a multiple correlation determination was made, using weight as the dependent variable and the four characters listed in table IV as the independent variables. The simple correlations, multiple correlation, and the partial regression coefficients of the F_2 generation of the Red Cherry x Golden Beauty cross are listed in table V. These were calculated by the methods described by Wallace and Snedecor (8).

It may be seen from table V that despite the sensible correlation between time of flowering and fruit weight ($.28 \pm .06$), there is apparently no inherent relationship between the two characters, since the partial regression coefficient ($-.026$) is so insignificant. Hence one may reasonably suspect that time of flowering in this particular cross has no fundamental influence on the weight of fruit. An average difference of two days (80.5 — 78.4 days) in table IV is considered of no practical significance. Also it is to be borne in mind that in this cross the larger Golden Beauty parent was somewhat later in maturity than the smaller Red Cherry parent.

Investigators of fruit size in tomatoes may be interested in the results of table V, since they are useful in determining which measurements of the tomato are most directly related to the ac-

tual weight of the fruit. Naturally the equatorial diameter is most closely associated with weight, the simple correlation in this case being .96 ± .01, which is considered as being unusually high. Polar diameter is next in importance with a correlation of .86 ± .02. Number of seed locules is third in importance with a correlation of .61 ± .04. Days to flowering is not so highly correlated with fruit weight in this material (.28 ± .06).

Probably the best comparison of the relative influence of each of the four characters in this cross may be gotten by considering their partial regression coefficients in table V. These coefficients are sometimes useful in determining the relative influence of any independent variable when the interrelations of these independent variables are taken into consideration. For example, whereas the polar diameter shows a high, simple correlation with fruit weight, it is apparent that some of this is due to the relations of this diameter with number of locules and with the equatorial diameter, since the partial regression coefficient of polar diameter on weight is surprisingly low in its relative value (.138). Evidently fruit weight in the tomato is largely controlled by the equatorial diameter (partial regression coefficient of .815), and only to a small extent by polar diameter. Number of seed locules and time of blooming have relatively no appreciable effect on weight when their partial regression coefficients are considered. These conclusions are verified in Bonny Best x Yellow Peach and New Globe x Yellow Cherry crosses to be discussed later. Were it not for the verification offered by these crosses one might suspect that the partial regression coefficients were somewhat misleading. It may be noted, however, that partial correlation determinations have led to similar conclusions with some of the same data.

Table V. CORRELATION DATA FROM THE F_2 GENERATION OF THE RED CHERRY x GOLDEN BEAUTY CROSS

Correlated variables	Simple correlation coefficients	Partial regression coefficients (weight as dependent variable)
Days to flowering		-.026
Polar diameter	.34 ± .06	
Equatorial diameter	.31 ± .06	
Number seed locules	.06 ± .07	
Fruit weight	.28 ± .06	
Polar diameter		.138
Equatorial diameter	.87 ± .02	
Number seed locules	.31 ± .06	
Fruit weight	.86 ± .02	
Equatorial diameter		.815
Number seed locules	.62 ± .04	
Fruit weight	.96 ± .01	
Number seed locules		.055
Fruit weight	.61 ± .04	
Coefficient of multiple correlation		.964 ± .005

The coefficient of multiple correlation ($.964 \pm .005$) is surprisingly high in view of the few characters dealt with. Had specific gravity been introduced into the complex it might have raised this coefficient slightly because weight of fruit is noticeably affected by specific gravity. This fact was suspected because of the surprising lack of curvilinearity in the regression lines. There was, for example, only a very slight suggestion of nonlinearity in the regression line of equatorial diameter on weight. One would naturally suppose that in dealing with a variable like weight in tomato fruits, which are spherical or ellipsoidal, any regression determination involving diameters and weight would exhibit a distinct curvilinear effect. A plausible explanation of its absence seems to have been discovered in the density of the fruits which apparently is directly dependent on the internal structure of the tomato fruit. It was noted that the larger fruits with their "meaty" core (endocarp and axillary placental tissue) and consequently less watery condition have relatively less weight than the smaller fruits. This situation was verified by determining the specific gravity of a few different sized fruits. It was found that the smaller Red Cherry type had a specific gravity of about 1.02, whereas the Golden Beauty variety averaged about 0.97 — 0.99. The Yellow Peach variety, which is inclined to be somewhat hollow at times, had a still lower specific gravity, 0.95 — 0.97. Specific gravity determinations were difficult to obtain accurately, mainly because of the varying degrees of maturity of the fruit, a factor which is extremely important in specific gravity.

Because of the apparent overwhelming influence of equatorial diameter on fruit weight, it was thought desirable to determine the interrelations of the other variables and weight when equatorial diameter was omitted. This being done, the partial regression coefficients were found to be modified as follows:

Time of flowering on weight 003
Polar diameter on weight 739
Number of locules on weight 377

Under such circumstances it is apparent that the variable, number of locules, is raised in importance as a determiner of weight and the same is naturally true of the polar diameter.

When time of flowering is dropped from consideration and only the three physical measurements of the fruit are used, the following partial regression coefficients are obtained:

Polar diameter on weight 134
Equatorial diameter on weight 809
Number of locules on weight 059

It is again evident that number of locules is a poor index of fruit weight among these three sets of measurements, and that polar diameter is diminished in importance.

It should be emphasized that, in crosses involving more radical differences with respect to the polar-equatorial diameter ratio, the polar diameter could very well exert a greater influence on fruit weight than it does in this varietal cross.

BONNY BEST X YELLOW PEACH CROSS

This varietal cross was included in these investigations primarily because it was the reverse of the preceding cross as in this case large size and the dominant color factors *R* and *Y* were contributed by the Bonny Best parent. Accordingly, if there is such a phenomenon as a genetic linkage between a color and a size factor, large size cannot, in this cross, be associated with the recessive *y* color factor as it was in the Red Cherry x Golden Beauty cross.

The parental varieties of this second cross had the following characteristics:

Bonny Best (large)—*RR YY* in color; 273.6 grams average weight.

Yellow Peach (medium) *rr yy* in color; 51.0 grams average weight.

An F_1 generation of 20 plants was orange-red (*Rr Yy*) in color, and produced an average fruit weight of 97.6 grams, indicating a slight dominance of the smaller size (see fig. 2).

Table VI. HYBRID GENERATIONS OF THE BONNY BEST (LARGE) x YELLOW PEACH (MEDIUM) CROSS SHOWING AVERAGE WEIGHT (GRAMS) OF FRUITS IN RELATION TO FLESH AND SKIN COLOR

Generation	Flesh color			Skin color		
	R	r	Difference	Y	y	Difference
F_2 generation RR YY x rr yy	90.9±1.3	88.5±2.6	2.4±2.9	92.6±1.4	83.4±2.1	9.2±2.5
No. of plants	118	30		113	35	
F_1 x Yellow Peach	72.1±1.2	69.9±1.1	2.2±1.6	73.3±1.2	68.5±1.1	4.8±1.6
No. of plants	79	101		93	87	
F_1 x Golden Beauty	119.4±4.4	113.1±4.2	6.3±6.0	116.0±4.4	117.3±4.3	-1.3±6.2
No. of plants	16	12		13	15	
Duplicated next year	99.3±2.5	100.5±2.1	-1.2±3.3	105.7±2.2	95.2±2.3	10.5±3.2
No. of plants	33	28		27	34	

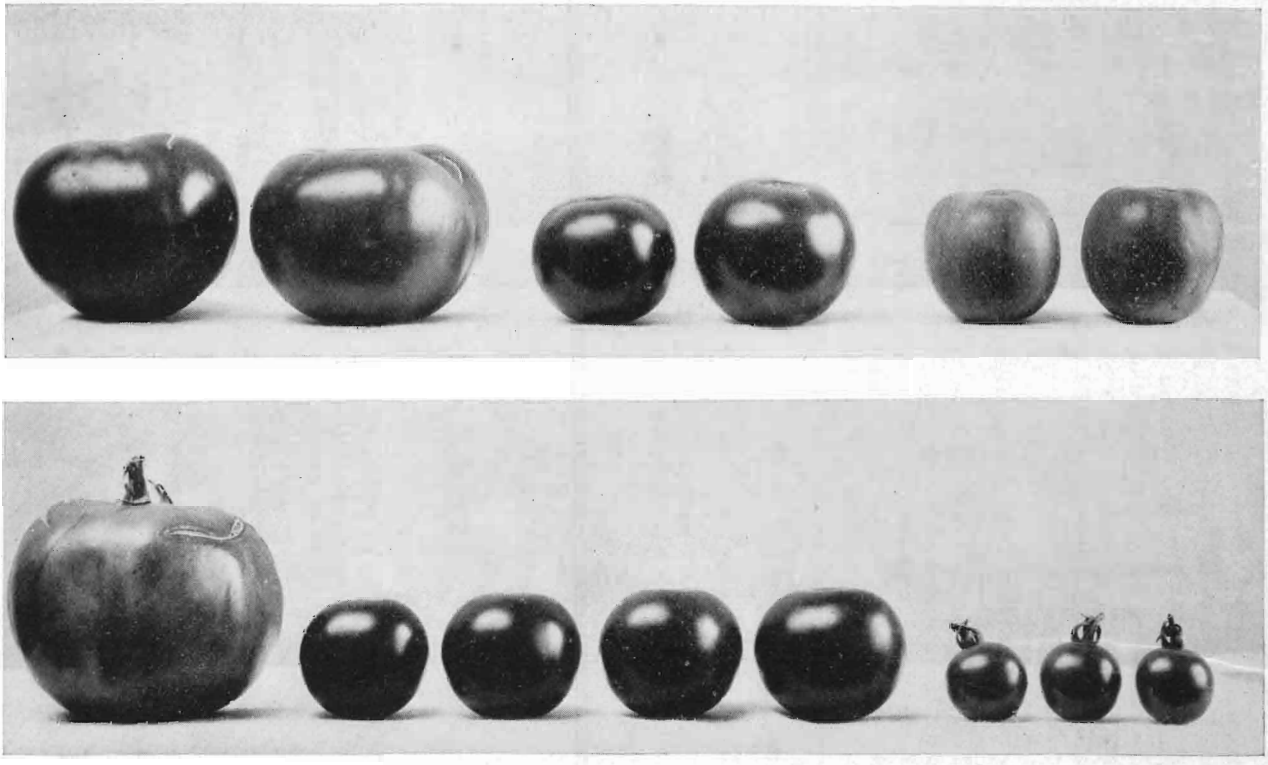

Fig. 2. Photograph of parents and first hybrid generation fruits, showing partial dominance of small size. Above (from left to right) Bonny Best (two fruits), first generation hybrids (two fruits) and Yellow Peach (two fruits). Below, New Globe (one fruit), first hybrid generation (four fruits) and Yellow Cherry (three fruits).

The F_2 and backcross generations which were grown in the field during the same season (1924) that the P_1 and F_1 generations noted above were duplicated, are arranged in table VI. As before, the average fruit weight for each of the two pairs of color factors has been determined.

Considering first the flesh color factors *R* and *r*, it is evident that in none of the hybrid generations is there any large difference in the average of the two color types. Three of the four plantings show a small difference in favor of the *R*-color class, but in no case is it statistically significant. If a linkage exists it is so small (or the cross-overs are so numerous) that it is obscured by the variations in the material.

When, however, the skin color factors *Y* and *y* in table VI are studied with reference to average weight of fruit, it is clear that the yellow-skinned types (*Y*) are noticeably heavier, with only one exception. In the exceptional case (F_1 x Golden Beauty) it will be noted that there were relatively few plants concerned, and that a duplicate planting made the following season resulted in a decisive increase in favor of the *Y*-type of fruits. With the one exception then, the dominant *Y* factor seems to be definitely correlated with larger size; and the differences when tested by their probable errors are dependable.

This relationship in the Bonny Best x Yellow Peach cross is offered as a verification for the existence of a genetic linkage between size and color factors discovered in the Red Cherry x Golden Beauty cross. It is considered as removing the possibility of explaining the correlation on a physiological basis, since in this cross the large size is associated with the dominant *Y* color factor, whereas previously the recessive *y* color factor had been found to be correlated with the larger size. Accordingly, it is felt that the reason for the association of *Y* and larger size in the Bonny Best x Yellow Peach cross is that the Bonny Best variety is carrying on the same chromosome the color factor *Y* and a factor for larger size or weight of fruit.

As a convenient manner of visualizing the relations between *Yy* and size, the frequency curves of the F_2 and backcross generations have been plotted in fig. 3. Here we have the same indications of segregation for size classes, especially apparent in the backcross generations. It will be noted that in all three distributions the yellow skinned (*Y*) fruits, shown by the solid line, are shunted to the right, an indication of greater weight.

In harmony with the presentation of data on the previous cross, table VII has been arranged in which characters other

BONNY BEST X YELLOW PEACH

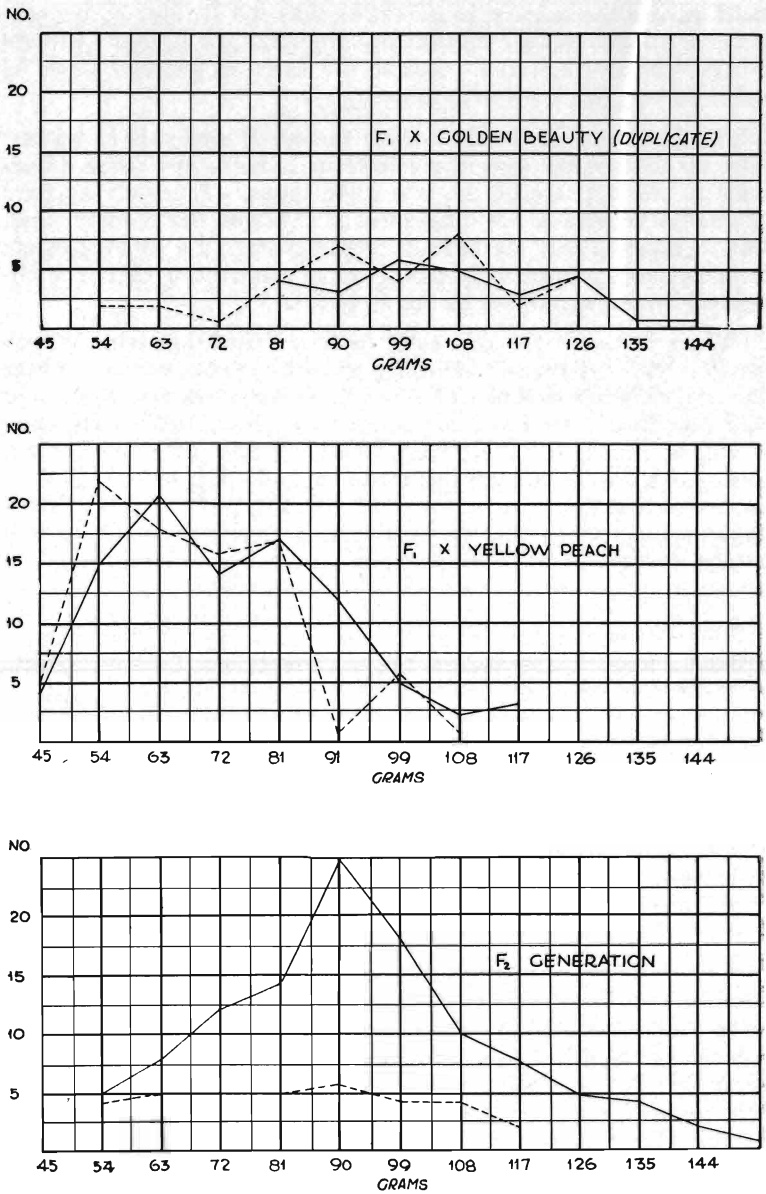

Fig. 3. Frequency curves of tomato weights in grams classed according to skin color types. Solid line represents dominant Y (yellow) skin and dotted line, recessive y (transparent) skin.

Table VII. RELATION OF SKIN COLOR FACTORS TO OTHER CHARACTERS IN THE BONNY BEST x YELLOW PEACH CROSS

Generations	Days to flowering		Days to harvest		Number of locules		Polar diameter mm.		Equatorial diameter mm.	
	Y	y	Y	y	Y	y	Y	y	Y	y
F_2 generation	66.0	66.2	117.1	117.6	3.6	3.2	47.4	47.3	57.6	55.5
F_1x Yellow Peach	67.0	71.0	118.1	118.6	3.3	2.9	44.2	42.5	53.2	51.4
F_1 x Golden Beauty	66.6	66.8	117.0	114.4	4.3	4.2	49.9	49.5	62.2	61.9
Duplicate planting	No data		No data		4.0	4.1	No data		No data	

than weight are shown in their relation to the *Yy* color factors. This table merely offers some verification for the fact that dominant *Y* in the Bonny Best x Yellow Peach cross is correlated more strongly with the greater weight than is *y*, as may be seen in the measurements of the fruits, other than weight. There are no consistent relations with time of flowering or maturity in this cross.

The simple correlations between these characters of table VII and weight of fruit, and also the multiple correlation coefficient together with the partial regression coefficients, have been calculated for the F_2 generation of this Bonny Best x Yellow Peach cross. These data are presented in table VIII.

There is a good, general agreement of the correlation data in this cross compared with that of the Red Cherry-Golden Beauty cross in table V. As before, the equatorial diameter has naturally the greatest influence on fruit weight, followed in turn by the polar diameter, number of seed locules, time of maturity and time of flowering. It is especially noteworthy that the last two characters had no influence on fruit weight when measured by their partial regression coefficients. In this cross neither time variable was significantly linked with fruit weight. There was a good correlation between the two, however ($.56 \pm .04$). The coefficient of multiple correlation was again exceedingly high ($.963 \pm .004$).

NEW GLOBE X YELLOW CHERRY CROSS

In this cross there is the interesting case of one dominant color gene being brought in by one parent and a second dominant color gene by the other parent. The parental color genotypes in this cross were *RR yy* and *rr YY*, and large size was contributed by the parent that carried the *R* and *y* color factors. The cross serves as a comparison or check of the first cross in which a Cherry type of tomato was also used.

Table VIII. CORRELATION DATA FROM THE F_2 GENERATION OF THE BONNY BEST x YELLOW PEACH CROSS[1]

Correlated variables	Simple correlation coefficients	Partial regression coefficients (weight as dependent variable)
Days of flowering		-.026
Days to harvest	.56±.04	
Polar diameter	-.03±.06	
Equatorial diameter	-.01±.06	
Number seed locules	-.01±.06	
Fruit weight	.05±.06	
Days to harvest		-.023
Polar diameter	.11±.06	
Equatorial diameter	.13±.05	
Number seed locules	.02±.06	
Fruit weight	.08±.06	
Polar diameter		.150
Equatorial diameter	.77±.02	
Number seed locules	.21±.05	
Fruit weight	.77±.02	
Equatorial diameter		.773
Number seed locules	.53±.04	
Fruit weight	.96±.01	
Number seed locules		.128
Fruit weight	.57±.04	
Coefficient of multiple correlation		.963±.004

[1]Calculations by K. M. Liu.

The actual weights concerned in this cross were as follows:

New Globe variety—*RR yy*—152.0 grams average.

Yellow Cherry variety—*rr YY*—3.1 grams average.

F_1 generation—*Rr Yy*—20.4 grams average.

Here again is the distinct, partial dominance of small size in the first hybrid generation (see fig. 2). The plants were all grown during the same season.

In the F_2 and backcross generations which appear in table IX, differences in average weight of fruits dependent upon their color

Table IX. HYBRID GENERATIONS OF THE NEW GLOBE (LARGE) x YELLOW CHERRY (SMALL) CROSS SHOWING AVERAGE WEIGHT (GRAMS) OF FRUITS IN RELATION TO FLESH AND SKIN COLOR

Generation	Flesh color			Skin color		
	R	r	Difference	Y	y	Difference
F_2 generation RR yy x rr YY	22.8±0.8	18.1±1.3	4.7±1.5	21.9±0.9	22.2±1.1	0.3±1.4
No. of plants	71	14		63	22	
F_1 x Yellow Peach	38.7±1.2	31.5±1.4	7.2±1.9	34.2±1.6	37.0±1.2	2.8±2.0
No. of plants	47	32		34	45	
F_1 x Golden Beauty	62.5±3.8	63.4±3.8	-0.9±5.4	48.8±1.9	86.0±4.4	37.2±4.8
No. of plants	26	24		31	19	
Duplicated next year	61.6±2.1	56.4±2.1	5.2±2.9	58.2±1.9	59.6±1.8	1.4±2.5
No. of plants	36	37		35	38	

NEW GLOBE X YELLOW CHERRY

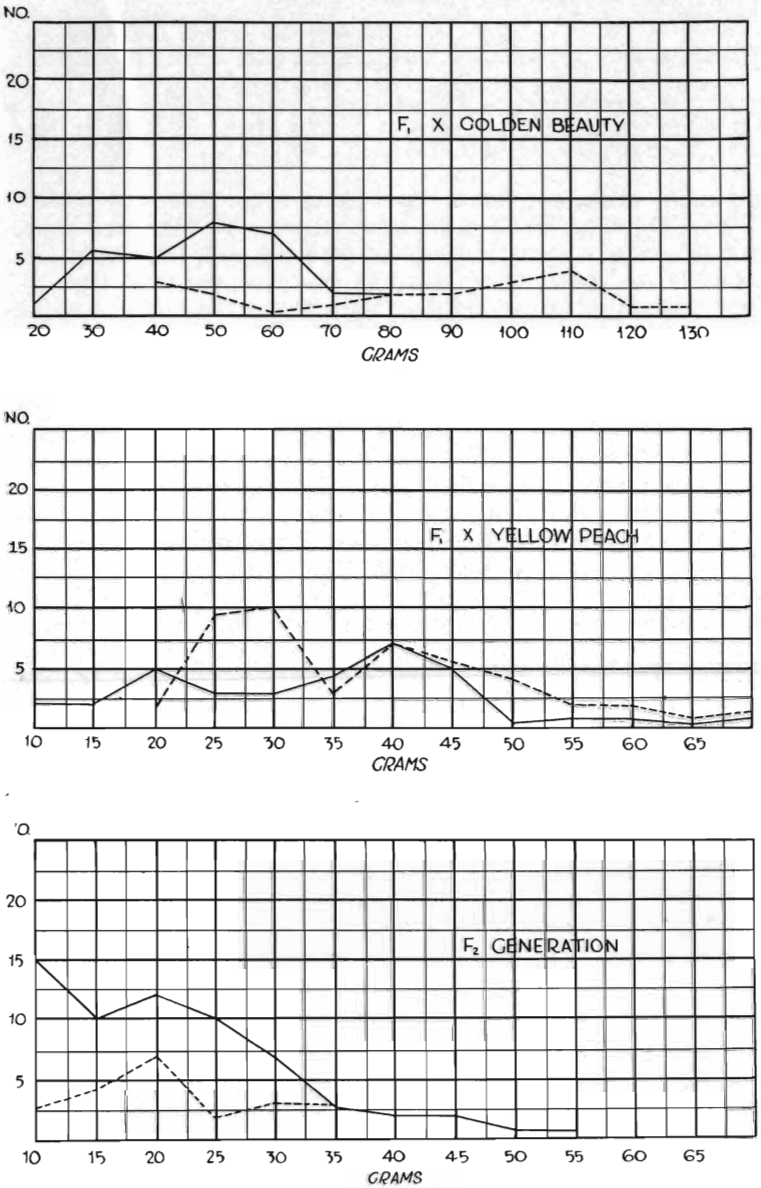

Fig. 4. Frequency curves of tomato weights in grams classed according to skin color types. Solid line represents dominant Y (yellow) skin and dotted line, recessive y (transparent) skin.

Table X. RELATION OF SKIN COLOR FACTORS TO OTHER CHARACTERS IN THE NEW GLOBE x YELLOW CHERRY CROSS

Generations	Days to flowering		Number of locules		Polar diameter mm.		Equatorial diameter mm.	
	Y	y	Y	y	Y	y	Y	y
F_2 generation	58.7	59.3	2.9	2.8	29.9	31.0	33.6	33.8
F_1 x Yellow Peach	63.6	64.3	3.2	3.0	34.0	35.9	39.5	40.8
F_1 x Golden Beauty	61.2	62.2	3.8	4.8	38.4	43.5	45.6	55.6

types are again apparent. As before, while there are no very large differences in the flesh color classes, yet there are appreciable and consistent indications that the red (R) fruit class tends to be larger, which is to be expected, perhaps, since the New Globe parent carried dominant R and the larger size. In two of these hybrid generations the differences are statistically significant.

With respect to skin color genes Y and y, it is again established that the color type brought in by the larger parent (New Globe—yy) was invariably associated with the larger fruits. This was true in all three hybrid generations, but only in the backcross with the Golden Beauty type was there a mathematical significance to such a difference in favor of the recessive y factor.

The graphs of these three hybrid generations showing the relation of size to the Yy color factors appear in fig. 4. While the F_2 averages in table IX were not greatly different, the linkage between y and larger size stands out clearly in the curve of fig. 4 in that very few of the smallest fruit classes are of the Y color type. The same situation occurs in the backcross generations.

Table XI. CORRELATION DATA FROM THE F_2 GENERATION OF THE NEW GLOBE x YELLOW CHERRY CROSS[1]

Correlated variables	Simple correlation coefficients	Partial regression coefficients (weight as dependent variable)
Days to flowering		.017
Days to harvest	.34±.08	
Polar diameter	.31±.08	
Equatorial diameter	.16±.09	
Number seed locules	-.04±.09	
Fruit weight	.20±.09	
Days to harvest		-.023
Polar diameter	.28±.08	
Equatorial diameter	.25±.08	
Number seed locules	.08±.09	
Fruit weight	.22±.08	
Polar diameter		.182
Equatorial diameter	.91±.02	
Number seed locules	.44±.06	
Fruit weight	.92±.01	
Equatorial diameter		.819
Number seed locules	.68±.05	
Fruit weight	.97±.004	
Number seed locules		-.001
Fruit weight	.63±.03	
Coefficient of multiple correlation		.979±.003

[1]Calculations by C. S. McCleskey.

Here are seen distinct evidences of size segregation in the multimodal nature of the curves.

The relations between the *Yy* color genes and characters other than weight have been arranged in table X as a matter of verification. Correlation data for the F_2 generation of this cross are given in table XI. The similarity of the simple correlation coefficients and the partial regression coefficients with those in the other two crosses is striking. It is again very apparent that number of locules plays no great part in fruit weight. The same may be said of the time of flowering or maturity. Since these same conclusions have been established in three crosses involving six different varieties, there may be some degree of generality in them.

MISCELLANEOUS CROSSES

Six additional crosses involving color and size differences have been tested in the F_2 generation, and the data are grouped in table XII. A detailed discussion of each cross is not essential, but a few salient features may be mentioned.

John Baer x *Yellow Peach*—With large size contributed by the John Baer variety (*RR YY*), no relation between flesh color and size is apparent. The skin color factors, however, show an appreciable influence of an association of *Y* and larger size, the difference not being statistically significant, however.

Dwarf Giant x *Yellow Peach*—In this cross with the larger, dwarf variety contributing the color genes *R* and *Y*, there is a consistent relation between *R* and greater weight in duplicate plantings. It is felt that this is sufficient evidence to indicate a slight linkage between the *Rr* color factors and size in this cross. The skin color genes exhibit no consistent relationship with size in the F_2 generations. However, when the F_1 plants of this cross were fertilized by the Yellow Peach and Golden Beauty varieties (*rr yy*) there was found a small, tho consistent correlation between both color factors and size. In the backcross to the Yellow Peach variety the following averages of fruit weight occurred in the progeny grown in the greenhouse:

Flesh color

Red (R) 38.2 grams (59 plants)
Yellow (r) 36.2 grams (61 plants)

Skin color

Yellow (Y) 38.8 grams (58 plants)
Colorless (y) 35.7 grams (62 plants)

The progeny from the cross of the F_1 plants on the larger Golden Beauty variety averaged as follows:

Table XII. F_2 GENERATIONS OF MISCELLANEOUS CROSSES SHOWING AVERAGE WEIGHT (GRAMS) OF FRUITS IN RELATION TO FLESH AND SKIN COLORS

Crosses	Flesh color			Skin color		
	R	r	Difference	Y	y	Difference
John Baer x Yellow Peach						
RR YY (large) x rr yy (medium)	74.1±1.2	73.9±2.1	0.2±2.4	74.8±1.2	70.9±1.9	3.9±2.3
Number of plants in field	108	37		116	29	
Dwarf Giant x Yellow Peach						
RR YY (large) x rr yy (medium)						
Grown in field	90.0±1.8	82.8±3.0	7.2±3.5	87.6±1.8	89.6±3.0	-2.0±3.5
Number of plants	88	32		91	29	
Duplicated in greenhouse	41.6±1.1	36.2±1.7	5.4±2.0	41.4±1.1	36.7±1.1	4.7±1.6
Number of plants	69	20		69	20	
Red Cherry x Yellow Peach						
RR YY (small) x rr yy (medium)						
Grown in field	16.8±0.05	16.1±0.05	-0.7±0.06	15.8±0.04	18.6±0.08	2.8±0.09
Number of plants	64	15		55	24	
Duplicated in greenhouse	12.0±0.2	11.5±0.3	-0.5±0.4	11.8±0.2	12.2±0.3	0.4±0.4
Number of plants	107	40		110	37	
John Baer x Golden Beauty						
RR YY (large) x rr yy (smaller)						
Grown in field	127.4±2.3	113.0±1.9	14.4±3.0	124.3±2.2	122.5±3.5	1.8±4.1
Number of plants	39	13		37	15	
Dwarf Giant x Yellow Cherry						
RR YY (large) x rr YY (small)	14.0±0.4	14.1±0.8	-0.1±0.9			
Number of plants in greenhouse	57	20				
Bonny Best x Yellow Cherry						
RR YY (large) x rr YY (small)						
Grown in field—1923	22.8	23.2	-0.4			
Number of plants	38	11				
Grown in greenhouse—1923	16.0	10.8	5.2			
Number of plants	33	6				
Grown in greenhouse—1924	12.7	14.2	-1.5			
Number of plants	63	17				

Flesh color

Red (R) 57.9 grams (81 plants)
Yellow (r) 54.1 grams (63 plants)

Skin color

Yellow (Y) 58.1 grams (71 plants)
Colorless (y) 54.5 grams (73 plants)

While the differences are in no case very large, their consistency gives some evidence of a slight linkage between both of the color factors and weight of fruit in this cross of a dwarf and a standard variety.

Red Cherry x *Yellow Peach*—This is a cross involving rather small types of fruits in which the larger variety carries the recessive color genes *r* and *y*. While no relation of any importance exists in the matter of flesh color, there is a marked increase of weight in the recessive *y* class of fruits in the field-grown planting. The difference in this one case is beyond doubt highly significant.

John Baer x *Golden Beauty*—This is a test involving the larger sort of fruits. A selection from the John Baer variety (*RR YY*) averaged 119 grams during the season (1925) when the F_2 generation in table XII was grown, whereas a strain of Golden Beauty variety (*rr yy*) had a mean weight of 109 grams. Thus *R* and *Y* were associated with the larger fruit in the parental generation. A statistically significant linkage between *Rr* and size seems to exist in this cross, since the red-fleshed fruits averaged 14.4 ± 3.0 grams more than the yellow-fleshed fruits. No skin-color linkage was apparent.

Dwarf Giant x *Yellow Cherry*—In this cross only the *Rr* color genes are involved, and the data give no evidence of any linkage.

Bonny Best x *Yellow Cherry*—The F_2 results of this cross are variable, pointing to no correlation between *Rr* and size. Seven different backcrosses of the F_1 of this cross to the Yellow Cherry variety also gave absolutely no evidence of linkage. It is very interesting to observe, however, that one backcross generation of 40 plants in which the Yellow Peach variety was used, instead of the Yellow Cherry, did show a correlation. In this case the *R* fruits averaged 32.6 grams and the *r* fruits 27.8 grams. This difference (4.8 ± 1.9) is an appreciable one and is significant to a fair degree. The same F_1 generation was also backcrossed to the larger, double recessive *rr yy*, Golden Beauty variety. A linkage between *Rr* and size again was brought out when the *R* plants averaged 60.4 grams and the *r* fruits 55.5 grams. This gives a difference of 4.9 ± 3.0 grams, which is scarcely signifi-

cant. These two backcrosses illustrate very well the usual isolation of size differences, especially small ones, whenever the dominance of the smaller varieties is offset.

DISCUSSION

Sufficient experimental data in the tomato have been presented to warrant the conclusion that genetic linkage exists between color and size factors. The evidence for linkage between size of fruit and color genes *Yy*, responsible for skin color of the tomato, seems to be indisputable. It occurred in seven different crosses.

In the progeny from the following parents, the dominant *Y* color factor was correlated with the larger fruit:

Bonny Best x Yellow Peach
John Baer x Yellow Peach
John Baer x Golden Beauty
Dwarf Giant x Yellow Peach

In most of the hybrid generations arising from these varietal crosses the difference in weight of fruit between the *Y* and *y* color classes in favor of the former was statistically significant.

The reverse situation occurred in the following crosses:

Red Cherry x Golden Beauty
New Globe x Yellow Cherry
Red Cherry x Yellow Peach

In all three crosses of this type, in which the larger size was contributed by the parent bringing in the recessive color gene *y*, there were conclusive evidences of linkage between size factors and the skin color factors *Yy*. For example, in the Red Cherry-Golden Beauty progenies the colorless-skinned fruits were practically 50 percent heavier than the yellow-skinned fruits.

Accordingly it is demonstrated that such linkages or correlations are genetic in nature and not physiological. In other words, the direction of the correlation or linkage was entirely determined by the manner in which the color genes and the size factors were contributed by the parental varieties. It is difficult to conceive of any other interpretation than that certain major size factors are borne on the same chromosome that carries the skin color genes *Yy*. Under such circumstances it seems entirely logical to believe that size characters depend on the same chromosomal mechanism that so ably accounts for color inheritance.

With respect to flesh color genes *Rr* there were less pronounced correlations with size. However, in five crosses a noticeable relationship was found. In four cases, it happened that the dominant color gene *R* was correlated with the larger fruits.

This occurred in the progeny of the following crosses:

Bonny Best x Yellow Peach
New Globe x Yellow Cherry
Dwarf Giant x Yellow Peach
John Baer x Golden Beauty

In only the second and fourth crosses were the differences statistically significant. In a fifth cross, Red Cherry x Golden Beauty, there was consistent evidence of a slight linkage between *Rr* and size, in which case the recessive color gene *r* was the one associated with the larger fruits.

It should be noted that in no case were such large size differences encountered with respect to the flesh color genes *Rr* as with the skin color genes *Yy*. It becomes of interest to speculate whether there may be any reason for the discovery of rather numerous and appreciable correlations of the *Yy* genes with size in contrast to the rarer cases of the *Rr* genes being linked with size factors. It is entirely possible that the nature of the chromosomes determines this difference. For example, the *Y*-chromosome may be smaller or of such a nature that cross-overs occur very infrequently, whereas the *R*-chromosome permits a larger degree of exchange of genes. Accordingly, it would be more difficult to detect linkage in the latter unless the color and size genes were very closely linked.

Thus it is established that the tomato chromosomes bearing the color genes *Rr* and *Yy* are also carriers of the size factors. It is rather interesting to observe that such a situation was confirmed in a goodly number of varieties. In these investigations no varietal crosses made by the writer have been omitted, so that it appears as if this fact were not an exceptional condition. Inasmuch as only 2 of the 12 pairs of tomato chromosomes, Winkler (11), are involved in this study, it would not be surprising to discover that the other chromosomes are similarly situated. In fact, a beginning of such a verification has already been made with respect to a third chromosome pair that carries the linked factors *Dd* (tall-dwarf) and *Pp* (smooth-"peach"). This case is reserved for a future report.

The proof afforded by these investigations on the tomato, coupled with the analagous cases in the inheritance of egg size in *Drosophila*, Warren (9), and in seed size of *Phaseolus*, Sax (5), Sirks (7), forces the conviction that the multiple-factor hypothesis of quantitative inheritance is on the road to verification. Such work points definitely to the actual existence of chromosomal genes controlling size characters. Similar cases will undoubtedly be discovered in other species of plants and animals. In this connection it may not be inapt to note an out-

standing example in maize which appears to offer additional evidence.

Among the numerous eight-rowed commercial varieties of corn, there are none apparently with red cob color; all are white-cobbed. Is this a mere coincidence, or does it mean that some inherent relation exists between cob color and row number? Preliminary tests have indicated that this situation also may be interpreted as a case of genetic linkage between color and size factors, since the inheritance of row number in maize is apparently dependent on multiple factors.

Attention should be called to the fact that in these crosses, involving a large and a small, or a large and a medium sized variety of tomato fruits, there was no evidence of major size factors which acted in a complementary fashion such as were found by P. A. Warren (10) for fruit shape or fasciation in tomatoes. No linkage between size and color was found in which the smaller parent, for example, contributed a factor for larger size of fruit. This, perhaps, might not be expected in crosses in which the F_1 generation fruits were smaller than the average of the parental types, in which no transgressive segregation occurred in the F_2 generation, at least as far as obtaining a plant with fruit as large or larger than the larger parent was concerned. Why detectable, complementary factors for fruit shape exist, and are apparently absent as far as fruit size is concerned is not apparent, unless it be due to the particular nature of the varieties used in combination with each other.

In this connection it may be noted that size characters in the tomato are somewhat peculiar in their F_1 behavior. Whereas the F_1 tomato plant ordinarily shows the marked vegetative vigor of heterosis, the F_1 fruits themselves are characteristically smaller than the parental average, thus exhibiting no heterosis. This has been attributed to the influence of the dominance of the factors for small size, a fact which is verified to some extent in the F_2 generation which shows some skewness, the mode being nearer the smaller end of the distribution. From this it may be argued that each size factor in the tomato exerts an effect, ordinarily with the phenomenon of dominance, and that strict complementary action, whereby one factor alone exercises no influence, is not characteristic of size in tomato fruits.

An experience of the writer with respect to his study of size inheritance is deemed of sufficient importance to justify comment, if only to aid other investigators doing similar work. Thruout these tomato investigations it may be noted that invariably the greatest differences in the color-size linkages were obtained in the backcrosses, especially those in which the homozygous parent was a larger variety. The apparent cause for this phe-

nomenon is the "unlocking" of the dominance of small size, characteristic of most tomato varietal crosses. There is ordinarily enough dominance exhibited in the F_2 generation so that size differences among the smaller fruit types tend to become obliterated. Accordingly, the backcross method of "breaking" this dominance by spreading the frequency distribution over a wider range, would seem to be helpful in attacking size inheritance under such circumstances. Backcrosses with the smaller, homozygous varieties have always proved disappointing in respect to analyzing size differences.

In the matter of choosing characters in the tomato for studies of size inheritance, the multiple correlation studies in tables V, VIII and XI should prove of some use to research workers. In the writer's experience, time of blooming and time of harvest (maturity of first-cluster fruits) in tomatoes have been rather variable things, primarily because of their sensitive reaction to temperature and sunlight. Even in the greenhouse under the most ideal conditions, a period of cloudy weather would noticeably disturb the relative time of flowering. Time of fruit maturity was made somewhat uncertain mainly because of the variation of the individual plant, whereby sometimes one fruit on the first cluster would ripen, followed by others, while at other times the remaining fruits on the first cluster would come to a standstill, and the second and third cluster fruits commence to ripen. The partial regression coefficients in all the crosses studied showed fairly clearly that neither of the above characters influenced the ultimate weight of fruit appreciably. This was true even in the New Globe-Yellow Cherry cross that involved wide differences of blooming and maturity.

Number of locules proved to be poorly related to fruit weight. This is taken to mean that the number of locules is not so important in determining fruit weight as is the actual structure within the fruit, including the thickness of the endocarp (ovary wall), the extent of the placental tissue, and the presence or absence of empty space sometimes found between the seed and endocarp. For example, in practically all of the crosses involving the Yellow Peach variety, it was noted that this variety contributed a characteristic of "hollow" fruits to some of the offspring. Apparently in this case the ovary wall grows too large for the enclosed placental tissue which bears the seeds. In such fruits, weights and diameter measurements are poorly correlated. For this reason either specific gravity readings or notes on the internal structure are necessary for exact determinations.

Polar diameter of the fruit was found to have a surprisingly smaller influence on fruit weight than the equatorial diameter, despite the fact that the simple correlations between polar diameter and weight were significantly high in value.

If the observations on color and size factors in these experiments are verified with the other chromosomes of this species so that size factors are finally located on all of the 12 tomato chromosomes, it becomes evident that size inheritance is so complex that it will probably never be solved satisfactorily by the crude methods in vogue at the present time. In other words, the isolation of specific size factors in F_2 generations of crosses of large and small types, even when tested in F_3 and later hybrid generations, becomes so involved that conclusive results are likely to be absent. This is especially true if the manner in which the various size factors interact in development is to be determined. The most plausible mode of attack would seem to be offered in the use of size-color linkages, developed by the backcross method. One disadvantage may be encountered here, unfortunately, and that is the possible occurrence of cross-overs. If such are found, however, another link in the chain of evidence pointing to the chromosomal nature of size determination will have been forged.

SUMMARY

Data on color inheritance in tomato fruits are summarized and proof offered that *Rr* and *Yy* color genes are independently inherited of each other, and accordingly reside on different pairs of chromosomes.

Conclusive evidence is presented to demonstrate that genetic linkage occurs between color factors and size factors. Specifically it was established that the *Yy* pair of color genes, controlling skin (epidermis) color in tomato fruits, are so associated with certain hereditary factors that control weight of fruits that a genetic linkage between the two presents the most plausible explanation for the correlation. Accordingly, it is suggested that in certain varieties of tomatoes the homologous chromosomes bearing the skin color factors *Yy* also contain major size factors.

Linkages between the *Rr* pair of color genes, determining the flesh colors of tomato fruits and size factors were also discovered. These were more infrequent, however, and not so clearly evident.

Multiple correlation studies involving the independent variables, time of flowering, days to maturity, polar and equatorial diameters of fruit and number of seed locules, and the dependent variable of fruit weight are discussed. Using the partial regression coefficients as indicators, it was found that time of flowering and days to harvest had no appreciable effect on weight of fruit. Number of seed locules had practically no influence on fruit weight. The two physical measurements, polar and

equatorial diameter, obviously determined fruit weight to a considerable extent, altho the influence of the polar diameter was surprisingly small in comparison with the equatorial diameter. It was found that the specific gravity of tomato fruits was variable, there being a tendency for the smaller fruits to have a higher specific gravity.

In general, it may be added that all the evidence in this report points rather clearly to the fact that hereditary factors for size characters depend on the same chromosomal mechanism which so competently determines the nature of color inheritance.

BIBLIOGRAPHY

(1) HALSTED, B. D.
1918. Reciprocal breeding in tomatoes. Jour. Heredity, **9**:169-173.

(2) HOSHINO, V.
1915. On the inheritance of the flowering time in peas and rice. Jour. Coll. Agric. Tohoku Imp. Univ. **6**:229-288.

(3) LINDSTROM, E. W.
1924. A genetic linkage between size and color factors in the tomato. Science **60**:182-183.

(4) LINDSTROM, E. W.
1925. Inheritance in tomatoes. Genetics **10**:305-317.

(5) SAX, KARL
1923. The association of size differences with seedcoat pattern and pigmentation in *Phaseolus vulgaris*. Genetics **8**:552-560.

(6) SAX, KARL
1924. The nature of size inheritance. Proc. Nat. Acad. Sci. **10**:224-227.

(7) SIRKS, M. J.
1925. The inheritance of seedweight in the garden bean. Genetica **7**:119-169.

(8) WALLACE, H. A., AND SNEDECOR, G. W.
1925. Correlation and machine calculation. Iowa State College, Official Pub. **23**:1-47.

(9) WARREN, D. C.
1924. Inheritance of egg size in *Drosophila melanogaster*. Genetics **9**:41-69.

(10) WARREN, P. A.
1924. Genetic studies in Lycopersicum. I. The heredity of fruit shape in the garden tomato. Papers Mich. Acad. Sci., Arts and Letters **4**:357-394.

(11) WINKLER, H.
1916. Uber die Experimentelle Erzeugung von Pflanzen mit Abweichenden Chromosomenzahlen. Zeitschr. Bot. **8**:417-531.